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Coward or braveheart: extreme habitat fidelity through hypoxia tolerance in a coral-dwelling goby

Göran E. Nilsson[1,*], Jean-Paul Hobbs[2], Philip L. Munday[2] and Sara Östlund-Nilsson[1]

[1]*Department of Biology, University of Oslo, PO Box 1051 Oslo, Norway* and [2]*School of Marine Biology and Aquaculture, James Cook University, Townsville, Australia*

*Author for correspondence (e-mail: g.e.nilsson@bio.uio.no)

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Summary

Coral reef fishes are not known for their hypoxia tolerance. The coral-dwelling goby, *Gobiodon histrio*, rarely leaves the shelter of its host coral colony. However, our measurements indicate that this habitat could become hypoxic on calm nights ($[O_2]$ minima=2–30% of air saturation) due to respiration by the coral and associated organisms. Moreover, at very low tides, the whole coral colony can be completely air exposed. Using closed respirometry in water, we found that *G. histrio* maintains O_2 uptake down to 18% of air saturation, and that it can tolerate at least 2 h at even lower O_2 levels. Furthermore, during air exposure, which was tolerated for more than 3 h, it upheld a rate of O_2 consumption that was 60% of that in water. The hypoxia tolerance and air breathing abilities enables this fish to stay in the safety of its coral home even when exposed to severe hypoxia or air. To our knowledge, this is the first report of hypoxia tolerance in a teleost fish intimately associated with coral reefs.

Key words: hypoxia, Gobiidae, air breathing, Great Barrier Reef, *Gobiodon histrio*.

Introduction

Coral reefs are structurally complex environments that provide a diverse range of habitats for fish. Many small reef-fishes are habitat specialists (Munday and Jones, 1998) and some of these species display unique adaptations to the habitats they occupy (e.g. anemonefishes; Allen, 1972). Among the most habitat-specialized fishes on coral reefs are coral-dwelling gobies from the genus *Gobiodon* that live among the branches of coral colonies, mostly from the genus *Acropora* (Patton, 1994; Munday et al., 1997).

Species of *Gobiodon* are arguably exceptionally cowardly fishes. They secrete a poisonous mucus, and are therefore probably inedible to most predators (Schubert et al., 2003). Nevertheless, they spend virtually their whole adult life in narrow spaces formed between the branches of *Acropora*, a shelter that should make them inaccessible to most predators. Moreover, the need to leave the coral to find a breeding partner is minimized by the ability to change sex in either direction. Thus, if two individuals of the same sex end up in a coral colony, one of them will change its sex unless other breeding partners are nearby (Munday et al., 1998).

In addition to shelter, corals also provide a site for reproduction, and for some gobies, a source of food (Patton, 1994; Nakashima et al., 1996). Coral colonies are a limited resource and there are significant consequences to individual fitness to inhabiting different species of coral (Munday et al., 1997; Munday, 2001). Consequently, there is intense competition for colonies of preferred coral species (Munday et al., 2001).

Although coral colonies are an essential resource for coral-dwelling fishes, they may also present unique problems that could jeopardize the survival of its inhabitants. Physiological studies have shown that coral tissue becomes hypoxic at night (Jones and Hoegh-Guldberg, 2001). It is therefore possible that water between the coral branches becomes hypoxic on calm nights because of the combined effects of the nocturnal cessation of photosynthesis, continued respiration of the coral (and associated organisms), and lack of convective water movements. Furthermore, the entire coral colony may be exposed to air during spring tides. For example, coral colonies on the reef flat at Lizard Island (Great Barrier Reef) may be completely air exposed for 1–4 h during exceptionally low tides that occur up to 30 times per year. Despite these potential problems, coral gobies rarely leave the shelter of their host coral colonies, even when corals are fully exposed at low tide. Staying there under such conditions could be considered an act of bravery.

In this study we investigated hypoxia tolerance in the broad-barred goby, *Gobiodon histrio*, a common coral-dwelling goby on the Great Barrier Reef (Munday et al., 1999). This goby exhibits a strong preference for colonies of *Acropora nasuta* (Munday et al., 1997, 2001). First, we estimated the nocturnal water O_2 level likely to be experienced by gobies inhabiting *A. nasuta* on calm nights. We then used closed-system

respirometry to test the ability of *G. histrio* to tolerate these levels of hypoxia and to tolerate the extended periods of air exposure experienced during low tides.

Materials and methods

Study species

There are two distinct forms of *Gobiodon histrio* Valenciennes, provisionally named *G. histrio 'histrio'* and *G. histrio 'erythrospilus'* (Munday et al., 1999). In the present experiments, individuals of both forms were examined. However, no significant differences were found in any of the parameters measured. Therefore, in the final experiment, where we examined O_2 uptake during air exposure, the data from the two forms where pooled to limit the number of experimental animals required.

The experiments were conducted in October 2002 at Lizard Island Research Station (LIRS) on the northern Great Barrier Reef (14°40′ S 145°28′ E). *G. histrio*, of both forms, weighing 0.43–2.02 g (*histrio* form) or 0.6–1.51 g (*erythrospilus* form), where collected by anaesthetizing them with a dilute solution of clove oil (50 ml clove oil, 40 ml ethanol and 400 ml of sea water) sprayed into the coral colonies they occupied. Anaesthetized fish were carefully placed in plastic bags and transported to the laboratory, where they rapidly recovered. The fish were kept in shaded out-door aquaria with a continuous supply of water pumped directly from the ocean (27–28°C). The water O_2 level varied between 86% and 101% of air saturation. They were fed daily with mysid shrimps *ad libitum*, but were starved for 24 h before any experiments. The fish were kept in the laboratory for at least one week before the experiments, which were carried out outdoors in shaded daylight (10.00 h to 18.00 h). Oxygen concentrations are given as percentage of air saturation (100% equals a P_{O_2} of 151 mmHg or 20.1 kPa). The collecting of fish and coral was approved by the Great Barrier Reef Marine Park Authorities and the experiments followed ethical guidelines from the University of Queensland.

Fish respirometry

Closed respirometry was conducted as described by Nilsson (1992, 1996). In this method, the test animal is placed in a sealed container and the rate at which the water O_2 level declines is measured continuously using an O_2 electrode (Fig. 2A). The closed respirometer used for water breathing was custom-made out of a Perspex cylinder (inner Ø=80 mm) with a variable volume of 150–250 ml. Each experiment took approximately 6–9 h. The O_2 level was monitored using a galvanometric O_2 electrode (a microprocessor controlled Oximeter 323A from WTW, Weilheim, Germany) and recorded with a Powerlab 4/20 (AD instruments, Castle Hill, Australia) connected to a Macintosh Power Book, using the program Chart 4.0 (AD instruments).

The chamber was submerged in a flow-through aquarium to maintain it at the ocean temperature (27–28°C). To ensure circulation in the chamber and over the electrode, a small magnetic propeller was attached to the tip of the O_2 electrode. The propeller was driven by a magnetic stirrer placed outside the aquarium. All fish settled down immediately and remained virtually motionless during respirometry. Consequently, the O_2 consumption ($\dot{M}_{O_2}$) during the first hour was not significantly different from that during the second hour. The experiment was terminated when the fish showed signs of agitation and difficulty maintaining equilibrium. All fish recovered within a few minutes. The microbial background respiration was measured daily and was negligible provided the respirometer walls were kept clean. The experiments were carried out in shaded daylight between 09.00 h and 17.00 h.

$\dot{M}_{O_2}$ in mg O_2 h^{-1} kg^{-1} fish wet mass, was plotted against water O_2 concentration ($[O_2]$), given as a percentage of air saturation. The critical O_2 concentration ($[O_2]_{crit}$) was determined by fitting two linear regression lines to the curve, one for the normoxic, O_2-independent, part of the curve, and one for the steeply falling hypoxic part (Fig. 2B). The point where these lines crossed was taken as the $[O_2]_{crit}$. The $[O_2]_{crit}$ is the concentration below which the fish is unable to maintain a resting $\dot{M}_{O_2}$ that is independent of the ambient $[O_2]$ (Beamish, 1964). The mean $\dot{M}_{O_2}$ between 70% and 100% of air saturation was considered to be the normoxic $\dot{M}_{O_2}$. The short period of activity-related increase in $\dot{M}_{O_2}$ that was sometimes seen immediately after the fish was introduced into the respirometer was excluded from the measurements used to determine normoxic $\dot{M}_{O_2}$.

For measuring $\dot{M}_{O_2}$ in air, we used the same set up, but the O_2 electrode was connected to a 12 ml air filled glass chamber (submerged in the aquarium). The fish was placed in the chamber together with 0.3 ml of water. This small amount of water was necessary to avoid distress and excessive mucous production by the fish. With the droplet, the fish rapidly settled down, pointing its mouth into the droplet. The partial pressure of O_2 in the chamber never fell by more than 10% (from 151 mmHg to 136 mmHg).

The ventilation rate of the fish was estimated by counting the opercular movements during respirometry.

In the measurement of O_2 debt after air exposure, six fish (both forms) were kept in the air respirometry chamber for 2 h, whereupon they were transferred to the water filled respirometer. The respirometer volume was set to 250 ml, and by opening valves, the water was exchanged repeatedly, every 1–1.5 h so that the $[O_2]$ never fell below 60% of air saturation.

Oxygen levels in coral

To estimate O_2 levels among the coral branches overnight, three colonies of *A. nasuta* (23, 25 and 26 cm in diameter, all approximately 9 cm high, and weighing 2.76, 2.84 and 3.22 kg, respectively) were collected on the reef by carefully breaking them lose at the base. Each coral colony was kept in a 240 liter plastic tank (105 cm diameter, 28 cm high) continuously supplied with fresh sea water (27–28°C). To estimate O_2 levels between the coral branches, an O_2 electrode (as described above) was inserted 6 cm into the center of the coral, between the branches. Because the inter-branch distance was only

5–10 mm, while the electrode has a diameter of 15 mm, one branch was removed to accommodate the electrode. Another electrode was placed in the tank 30 cm from the coral. No stirrers were attached to the electrodes (to avoid creating water movements). Consequently, they were found to give readings that were 37.5% lower than those from stirred electrodes. The data were corrected for this deviation, which was found to be constant over the $[O_2]$ range of interest.

To simulate calm nights when the most severe nocturnal hypoxia is likely to occur, O_2 measurements were conducted in an outdoor tank with the water supply turned off to prevent convective water currents. Two measurements, on subsequent nights, were taken for each of the corals. Corals were returned to their original sites and secured to the reef.

Statistics

All values given are means ± S.E.M. Possible differences between the two forms were tested with the Wilcoxon test, while points in time series were compared using Friedman's non-parametric test for repeated measures followed by Dunn's post test (InStat 2.01 for Macintosh).

Results

Oxygen in coral

From sunset, $[O_2]$ declined between the coral branches and in the tank (Fig. 1). In the early morning, the average $[O_2]$ minimum in the coral was about 20% of air saturation, with the individual minima ranging between 2.2 and 30.9%. In two instances, the $[O_2]$ in the coral fell below 10% for about an hour in the early morning. Starting about 1 h after sunrise, photosynthetic O_2 production rapidly drove the $[O_2]$ in the coral to normoxic levels.

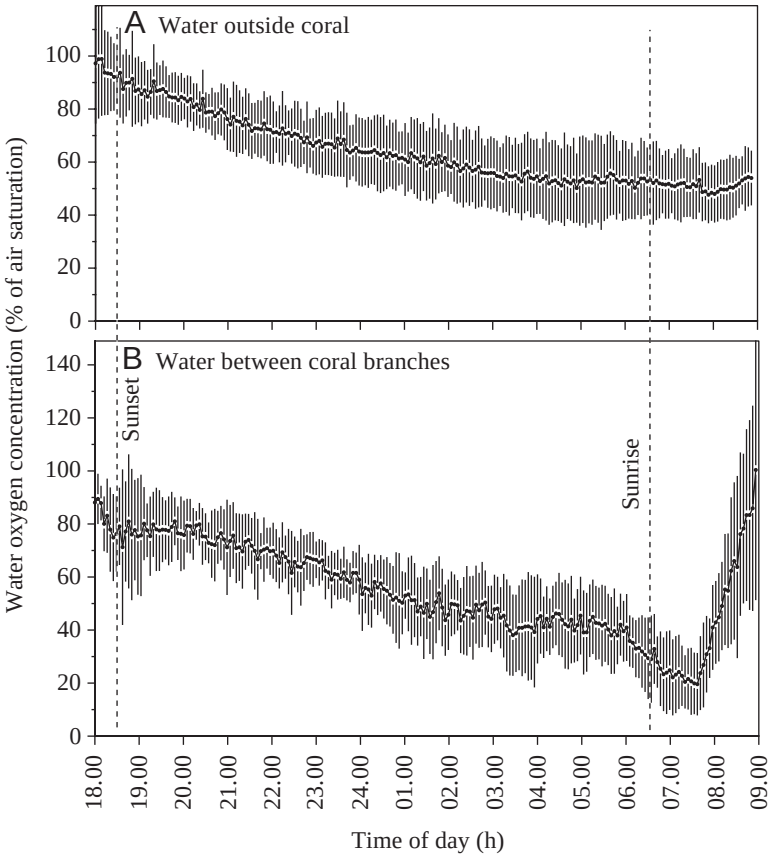

Fig. 1. Oxygen level (A) outside and (B) between branches of *Acropora nasuta* colonies from dusk to dawn. Values are means ± S.E.M. from six measurements on three corals. Sunset and sunrise are indicated by broken lines.

Respiration in water

From the respirometric measurements in water, we determined four variables: normoxic $\dot{M}_{O_2}$, $[O_2]_{crit}$, the O_2 level where the fish lost its equilibrium, and the time that elapsed between $[O_2]_{crit}$ and loss of equilibrium (Fig. 2A,B). These data are summarized in Table 1.

G. histrio was extremely hypoxia tolerant. Its $[O_2]_{crit}$ was 18.3±1.4% of air saturation, and it tolerated a further 2 h of falling O_2 levels before showing signs of equilibrium loss at approximately 3% of air saturation (Table 1). All fish recovered their ability to maintain equilibrium within a few minutes in normoxic water.

G. histrio increased its ventilatory rate significantly in response to falling water $[O_2]$ until $[O_2]_{crit}$ was reached, whereupon the rate fell (Fig. 2C). As with the earlier results, there were no significant differences between the two forms of *G. histrio* (Fig. 2C includes both forms).

Table 1. *Variables measured using closed respirometry*

	histrio form	*erythrospilus* form	Both forms
$\dot{M}_{O_2}$ (mg kg^{-1} h^{-1})	259±83 (5)	237±54 (6)	247±20 (11)
$[O_2]_{crit}$ (% of air saturation)	20.9±5.5 (5)	16.1±2.4 (6)	18.3±1.4 (11)
$[O_2]$ at loss of equilibrium (% of air saturation)	3.0±0.6 (5)	2.7±0.6 (6)	2.8±0.4 (11)
Time between $[O_2]_{crit}$ and loss of equilibrium (min)	146±37 (5)	113±17 (6)	128±20 (11)
$\dot{M}_{O_2}$ in air (mg kg^{-1} h^{-1})	150±39 (5)	142±38 (6)	145±11 (11)

Values are means ± S.E.M. Number of fish is given within parentheses. There were no significant differences between the two forms (Wilcoxon test).

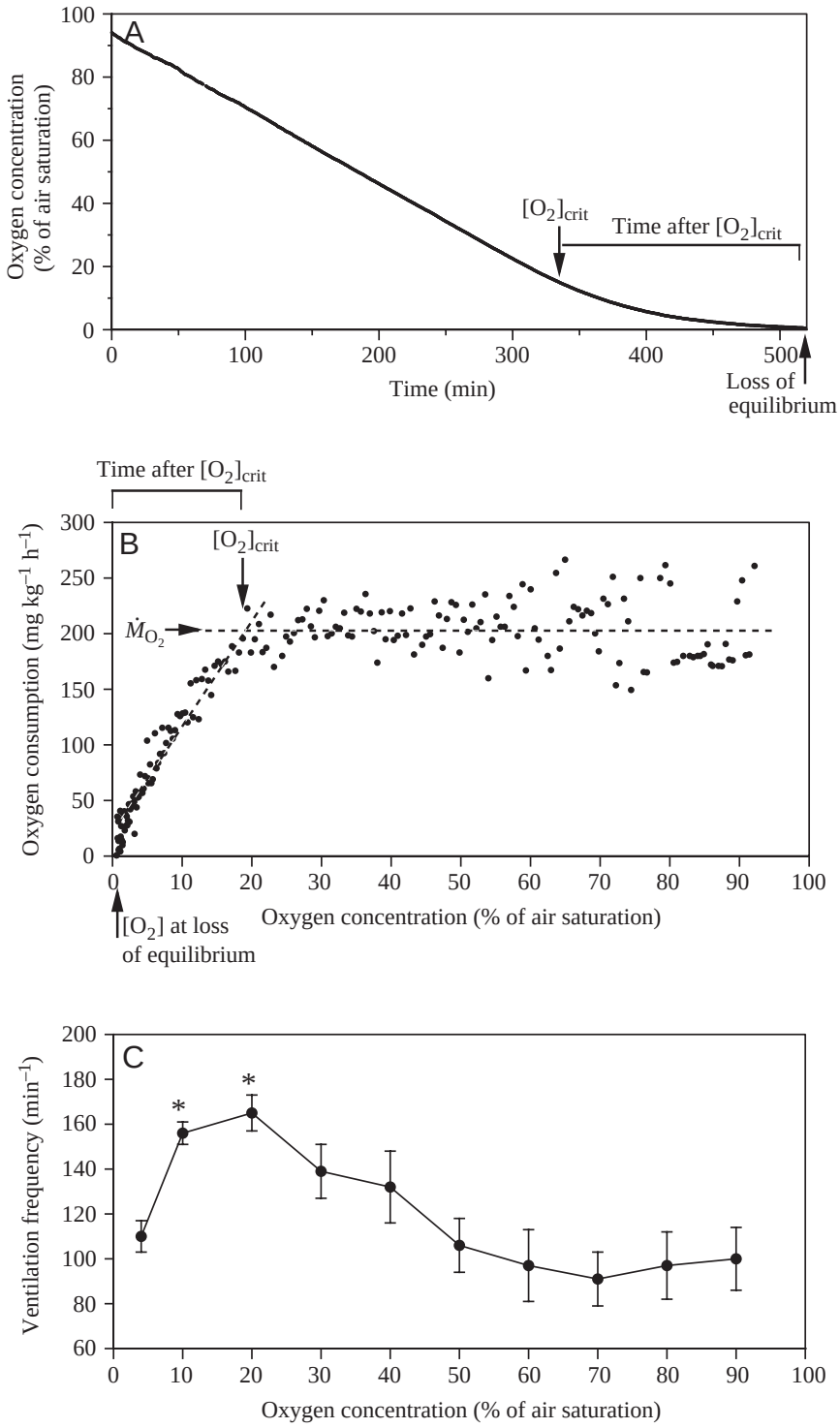

Fig. 2. (A) A recording of falling $[O_2]$ in the closed respirometer. (B) The graph is derived from A and shows the O_2 consumption at different levels of ambient $[O_2]$. Variables derived from the measurements of O_2 consumption in *G. histrio* are indicated in A and B. $\dot{M}_{O_2}$ is the normoxic O_2 consumption, and $[O_2]_{crit}$ is the critical O_2 concentration (below which the animal loses the ability to regulate its O_2 consumption). (C) The ventilatory frequency at different O_2 concentrations measured during respirometry (means ± S.E.M. of 11 individuals of both forms of *G. histrio*). A and B are from a typical animal, and the variables measured from several animals are given in Table 1. **P*<0.05 compared with any of the 70%, 80% and 90% values (Dunn's test).

Respiration in air

G. histrio showed a remarkable ability to take up O_2 in air, only accompanied by a drop (0.3 ml) of water. The ventilatory movements apparently circulated this small volume of water, by moving it over the gills and out through the opercular openings, from where it flowed back to the mouth.

$\dot{M}_{O_2}$ and ventilatory rate were maintained in air for at least 3 h (Fig. 3). The fish did not display any aberrant behavior when returned to water, which also applied to one individual that was kept in air for 4.5 h. The mean $\dot{M}_{O_2}$ of 11 individuals kept in the air filled respirometer for an hour was 145±11 mg kg^{-1} h^{-1} (Table 1), which was about 40% lower than that in water.

Oxygen debt

Since the $\dot{M}_{O_2}$ in air was 40% lower than that in water, we examined the possibility that the fish accumulate an O_2 debt during air exposure. After 2 h in air, *G. histrio* showed a significantly elevated $\dot{M}_{O_2}$ (P<0.001) during the first hour in water, as compared to the fourth, fifth and sixth hour (Fig. 4). $\dot{M}_{O_2}$ appeared slightly elevated during hours two and three, while by the fourth hour, it was virtually identical to the $\dot{M}_{O_2}$ of 247±20 mg kg^{-1} h^{-1} previously measured (Table 1). The total overshoot in O_2 consumed during the three first hours was 181±34 mg kg^{-1}. This was very similar to the expected O_2 debt of 204 mg kg^{-1} accumulated over 2 h in air (calculated by subtracting the $\dot{M}_{O_2}$ in air from the $\dot{M}_{O_2}$ in water and multiplying by the number of hours in air).

Discussion

Coral reefs are not usually considered to be hypoxic environments. However, we found that coral colonies inhabited by obligate coral-dwelling gobies can become severely hypoxic under calm conditions at night. The average $[O_2]$ minimum reached in the preferred coral species inhabited by *G. histrio* was similar to the $[O_2]_{crit}$ of *G. histrio*, i.e. about 20% of air saturation. Clearly, the ability of *G. histrio* to tolerate this level of hypoxia is an important prerequisite for it to remain sheltered among the coral branches at night. It should be pointed out that our measurements of water $[O_2]$ in coral colonies were done in a tank

without water movements to simulate the most extreme conditions during calm nights. Coral reefs are often swept by surge and tides which should counteract stagnant hypoxia inside the coral colony and it remains to be studied how common and severe hypoxia is in this habitat in nature. Coral colonies inhabited by *G. histrio* may also become completely exposed to air for 1–4 h during spring tides, but the fish does not leave the coral colony during these events (P.L.M., unpublished observation). The ability of *G. histrio* to survive in air clearly enables it to remain sheltered among the branches of its host coral colony even when it is no longer surrounded by water. To our knowledge this is the first documented case of habitat fidelity through hypoxia tolerance in a coral reef fish.

With regard to $[O_2]_{crit}$, there seems to be few comparable measurements of hypoxia tolerance in tropical sea fishes at temperatures close to 30°C (but see Nilsson and Östlund-Nilsson, in press). Data in the literature allow an interesting comparison with some species of cichlids living in African lakes (Verheyen et al., 1994; Chapman et al., 1995). These fishes, which are renowned for their hypoxia tolerance, have a $[O_2]_{crit}$ of about 20% of air saturation at 25°C – very similar to that displayed by *Gobiodon histrio*.

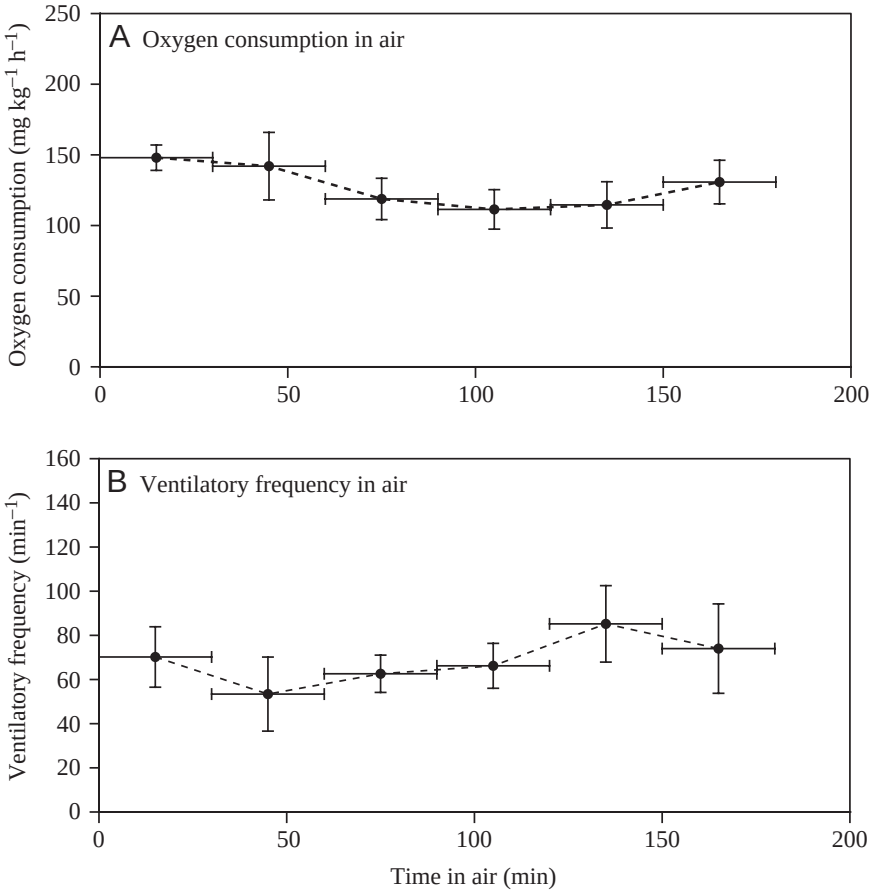

Fig. 3. (A) Oxygen consumption and (B) ventilatory frequency in *G. histrio* during air exposure. Both parameters were measured over 30 min periods, as indicated by the horizontal bars. Values are means ± S.E.M. from five animals.

Coral colonies are an essential resource for coral-dwelling gobies. Owing to their small body size, coral gobies could experience a high risk of predation (if edible to some predators) or hazardous predation attempts outside their host coral colonies. Thus, the ability to remain within the coral colony at night is likely to be a distinct fitness advantage. Coral colonies are also a limited resource for coral-dwelling gobies and there is intense competition for preferred corals at Lizard Island (Munday et al., 2001). Leaving the host coral during periods of hypoxia would provide opportunities for other individuals to usurp habitat space. Therefore, it would be advantageous for *G. histrio* to remain within the host coral colony at all times to defend it from competitors. Consequently, it appears that hypoxia tolerance in this goby is an important attribute to both reduce the risk of predation or predation attempts and limit the potential of losing vital habitat space.

There are other noteworthy examples of fishes that utilizes hypoxia tolerance for predator avoidance. The hypoxia tolerance of fishes of deep swamp refugia in the Lake Victoria region is probably important for modulating the impact of the predatory Nile perch (*Lates niloticus*) (Chapman et al., 2002). The most extreme example of predator avoidance through hypoxia tolerance is that of the crucian carp (*Carassius carassius*).

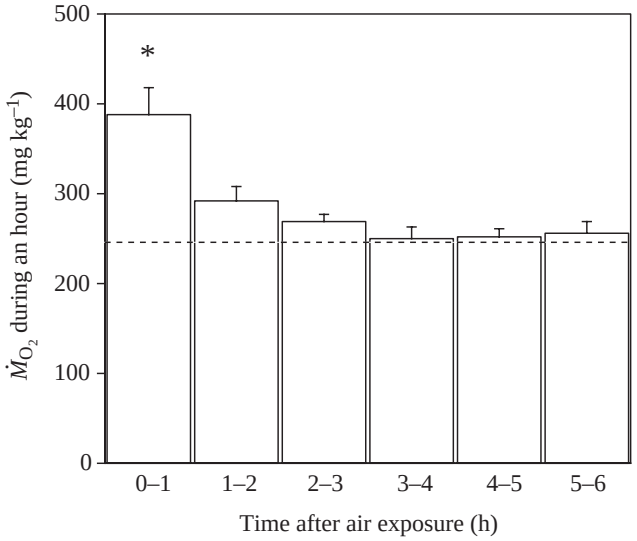

Fig. 4. Oxygen debt after air exposure in *G. histrio*. The values are O_2 consumption ($\dot{M}_{O_2}$) in water measured during 1 h periods immediately after exposure to air for 2 h. Means ± S.E.M. of six fish. The broken line shows the mean $\dot{M}_{O_2}$ previously measured in 11 individuals not exposed to air (from Table 1). *P<0.001 compared with the 3–4 h, 4–5 h and 5–6 h values.

Owing to its exceptional anoxia tolerance (Nilsson, 2001), the crucian carp is often the only piscine inhabitant in small lakes and ponds in Northern Europe, thereby completely avoiding predatory fish (Poleo et al., 1995; Holopainen et al., 1997).

Hypoxia tolerance is known in some gobiids, particularly estuarine species in temperate water (Graham, 1976; Gee and Gee, 1995; Martin, 1995). Tolerating hypoxia is less challenging in temperate waters than in tropical waters because $\dot{M}_{O_2}$ increases and water O_2 content falls with increasing temperature. The most hypoxia-tolerant gobiid is probably the Californian blind goby, *Typhlogobius californiensis*, that can survive 80 h of anoxia at 15°C (Congleton, 1974). However, hypoxia tolerance has also been reported in *Valenciennea longipinnis*, a burrowing goby that lives in sandy areas near coral reefs (Takegaki and Nakazono, 1995). The presence of hypoxia tolerance in both tropical and temperate gobies, from a wide range of genera, suggests that this may be an ancestral trait. Being phylogenetically pre-adapted to a hypoxic habitat may have been a prerequisite for the *Gobiodon* ancestors to become coral dwellers.

G. histrio was able to tolerate many hours in air. Mudskippers are the best known gobiid air breathers, some of which show specialized respiratory epithelia in the buccal cavity (Al-Kadhomiy and Hughes, 1988). A preliminary examination of the buccal cavity of *G. histrio* did not reveal any specialized respiratory epithelium or highly vascularized areas in the buccal cavity that would indicate morphological adaptations to air breathing. The likely mechanism used by *G. histrio* for O_2 uptake in air is the circulation of a small volume of water through the mouth and over the gills, as was observed in the respirometer. When water moves on the outside, from the opercular opening to the mouth, it would be oxygenated through diffusion from air. *G. histrio*, and some other coral-dwelling gobies, have a groove under each side of the jaw, running from near the opercular opening to near the front of the mouth (Harold and Winterbottom, 1999). This groove may assist in the circulation of water between the mouth and operculum.

Uptake of O_2 in air may also occur through the skin. Under the stereo microscope, we observed superficial capillaries in the skin, and many fishes, including gobies, have been shown to utilize cutaneous respiration both in water and air (Graham, 1976; Martin, 1995).

In *G. histrio*, $\dot{M}_{O_2}$ in air was about 40% lower than $\dot{M}_{O_2}$ in water, and during air exposure, this goby accumulated an O_2 debt that very closely correlated to the reduced uptake of O_2 during air exposure. This indicates that it relied on anaerobic metabolism to some degree during air exposure. The accumulation of an anaerobic end product (most likely lactate) will limit the time this fish can remain in air.

To conclude, tolerance to hypoxia and air exposure in *G. histrio* appear to reflect important adaptations that are needed to allow the highly specialized life style of most coral gobies. These abilities should make it possible for these fish to stay indefinitely in the shelter of their host corals, regardless of nocturnal hypoxia and periodic air exposure during very low tides.

To our knowledge, this is the first report of an extremely hypoxia-tolerant teleost intimately connected to coral reefs. However, recent results suggest that hypoxia tolerance, albeit to a lesser degree than that displayed by *Gobiodon histrio*, may be widespread among coral reef fishes (Nilsson and Östlund-Nilsson, in press). Moreover, a coral reef elasmobranch, the epaulette shark (*Hemiscyllium ocellatum*), has proved to be hypoxia tolerant. On Heron Island (Great Barrier Reef), the epaulette shark survives several hours of hypoxia (10–20% of air saturation) as the water of the shallow reef platform becomes cut off from the ocean at nocturnal low tides (Routley et al., 2002). In view of the exceptionally diverse life styles and habitats found on coral reefs, it is possible that hypoxia, and hypoxia tolerance, are more common phenomena on coral reefs than generally imagined.

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